An investigation into the buried viable seeds occurring across a successional series in the Magnesian Limestone of County Durham.

A study presented in part-fulfilment of the requirements for the degree of Master of Science (Ecology) of the University of Durham.

by

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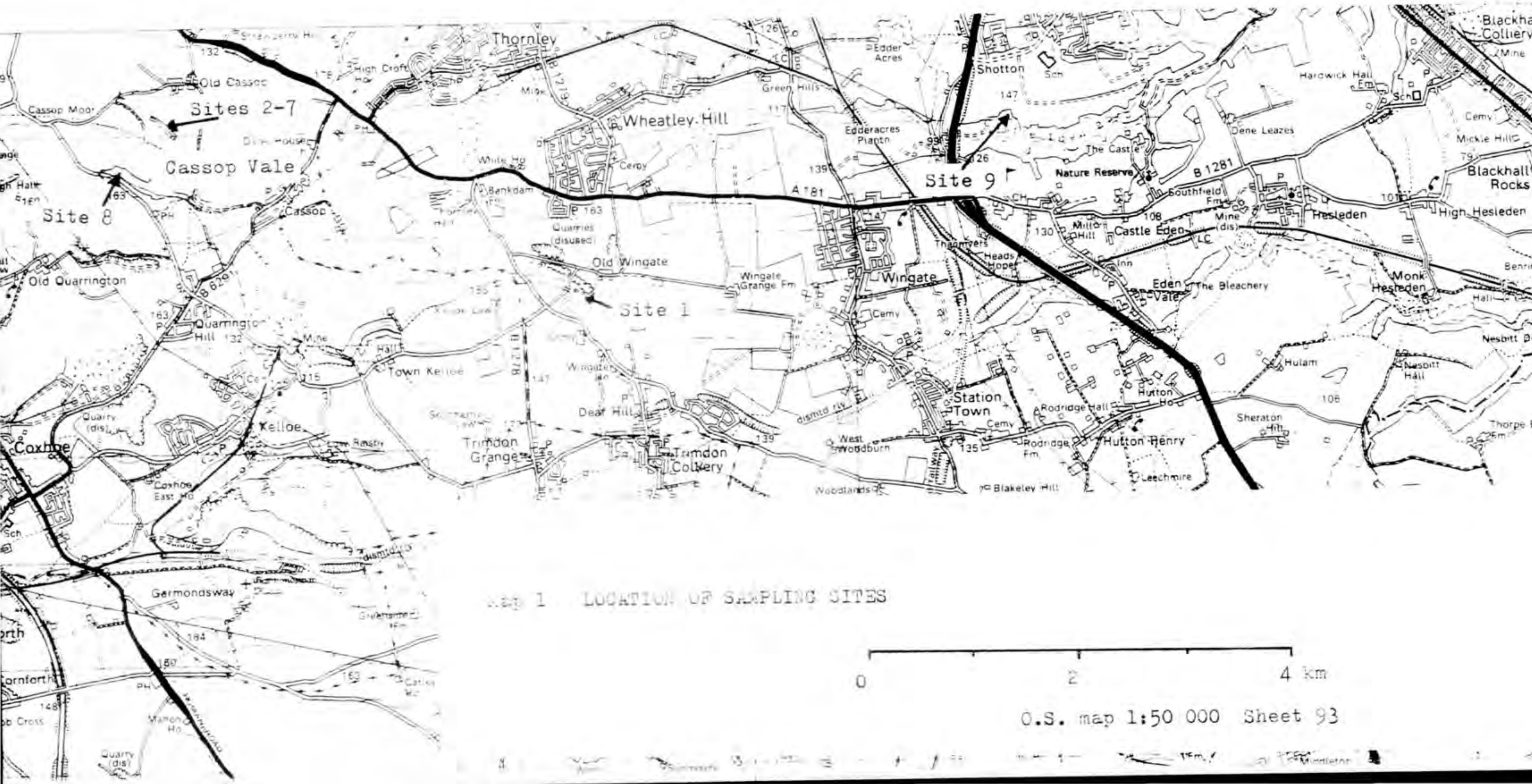
INTRODUCTION

Most investigations of buried seeds in Britain have been concerned with agriculture in both arable fields and upland and lowland pastures (Brenchley 1918, Chippendale and Milton 1934, Milton 1939, Champness and Morris 1948) so one has to turn to American literature for work describing buried seeds in natural vegetation across a successional series (Oosting and Humphreys 1940, Livingston and Allessio 1968, Johnson 1975).

Succession is a concept which has stimulated much ecological investigation but, whereas early studies of succession were primarily concerned with describing the sequence of species that successively invaded a disturbed site, (Cowles 1901, Clements 1916) more recent ones have focussed on the place of physical stress and competition for resources as factors controlling the course of succession. (Connell 1972, Horn 1976, Connell and Slatyer 1977).

This study embraces something of each of these approaches: it describes the density and distribution of buried viable seed across a successional series in the Magnesian Limestone of Co. Durham, relating these findings to those describing some successional series in North America, (Livingston and Allessio 1968, Oosting and Humphreys 1940) and it attempts to consider the role of buried seed in germination strategies developed in response to gradients of stress and disturbance across the series. In addition, the relevance of the conclusions to some conservation problems is briefly considered.



Map 1 LOCATION OF SAMPLING SITES

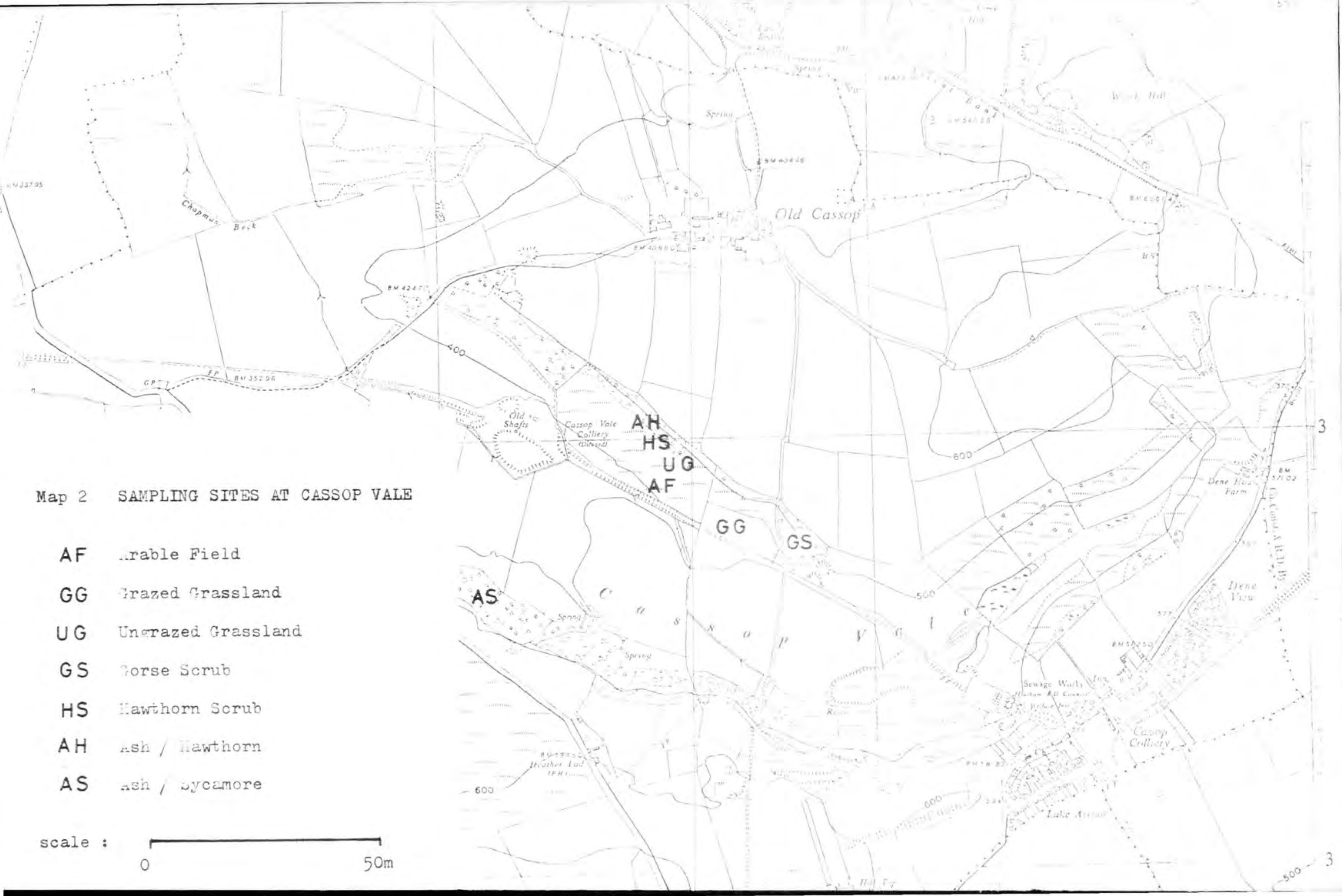
CHAPTER I : DESCRIPTION OF SITES AND METHODS OF INVESTIGATION

1.1 Selection of the sites

In Britain a dearth of areas of 'natural vegetation' severely limits the choice of suitable sites for an investigation into a successional series. Natural woodland of mature age has been utilized for centuries by man in a variety of ways, so that most woodland which remains is small in area and secondary in character. However, Cassop Vale (NZ 3338) a Nature Conservancy S.S.S.I. site, Grade 2, of 80 ha. has 'a full successional sequence from grassland to scrub and then to secondary woodland'. (Radcliffe 1977). This, together with a site in mature oak woodland at Castle Eden Dene (NZ 4138) and one in an abandoned quarry at Wingate (NZ 3737), provided a suitable range of 9 sites on the Magnesian Limestone in Co. Durham. The quarry is 4 km. from Cassop and the oak woodland 8 km. away. (Map 1)

Cassop Vale is one of the 'bays' produced by denudation of the western scarp edge of the Magnesian Limestone as it traverses the Coal Measures. (Heslop-Harrison and Richardson 1952). The central part of the valley has been much disturbed by mining: colliery waste is still visible near former coal shafts and the slopes on both sides have been locally quarried for stone and sand. Part of the floor of the valley at the E end is occupied by sewage works, the adjacent fields being used for grazing. A cereal crop (barley) occupies the W end of the valley floor. Secondary woodland and scrub grows on both the northern and southern valley sides.

Seven sites were selected for investigation within Cassop Vale:



Map 2 SAMPLING SITES AT CASSOP VALE

AF	Arable Field
GG	Grazed Grassland
UG	Ungrazed Grassland
GS	Gorse Scrub
HS	Hawthorn Scrub
AH	Ash / Hawthorn
AS	Ash / Sycamore

scale : 0 — 50m

Site 2	:	Arable field	(AF)
Site 3	:	Grazed grassland	(GG)
Site 4	:	Ungrazed grassland	(UG)
Site 5	:	Gorse scrub	(GS)
Site 6	:	Hawthorn scrub	(HS)
Site 7	:	Ash with Hawthorn	(AH)
Site 8	:	Ash with Sycamore	(AS)

Sites 2 to 7 were located on the N side of the valley, Site 8 on the South. (Map 2)

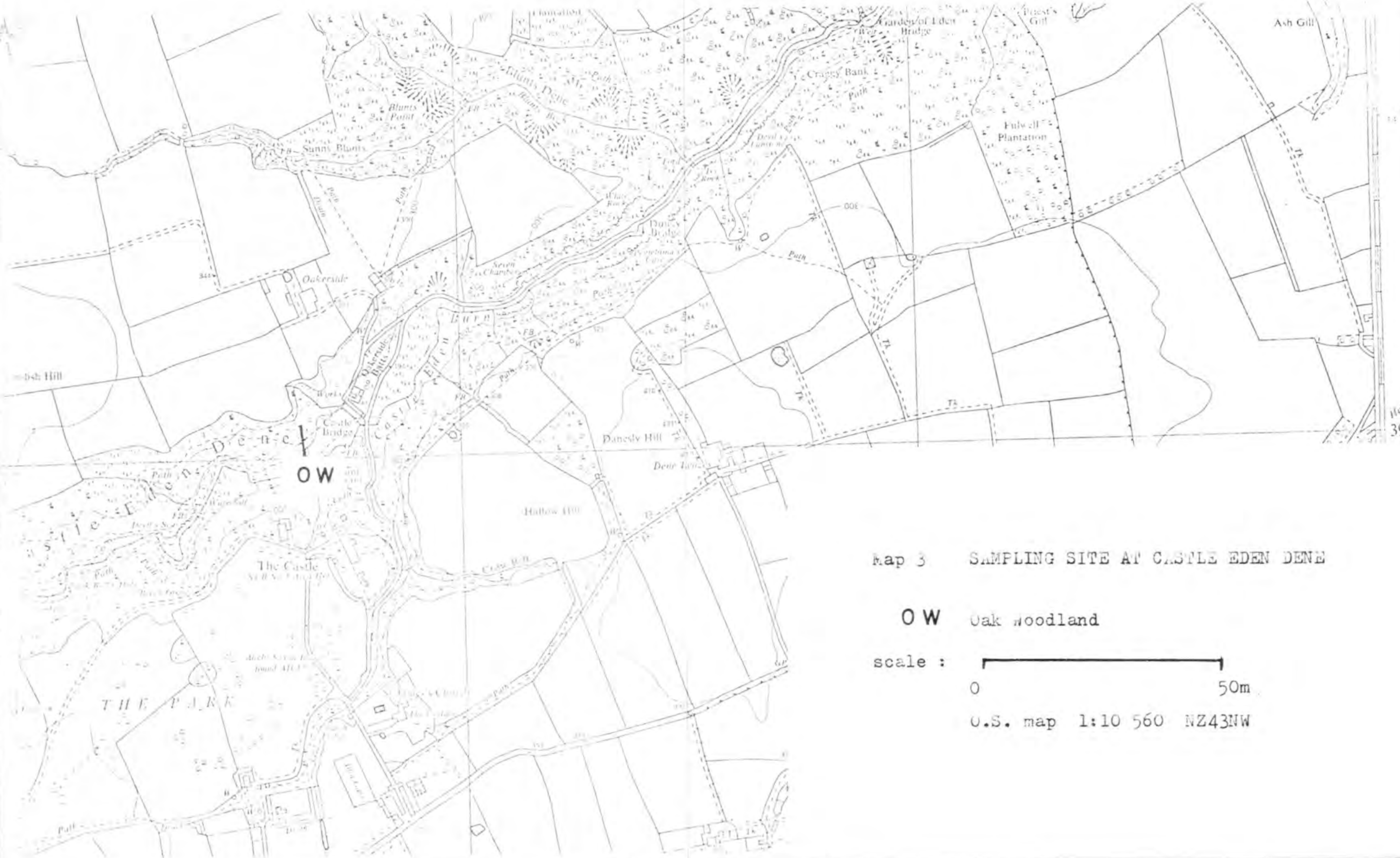
Quarrying at Old Wingate Quarry ceased about 15 years ago and the quarry was then abandoned. Subsequently, in relatively undisturbed conditions the natural vegetation had colonized the bare rock and provided a site with characteristics of the early stages of succession. A site characteristic of the other end of the succession series was found at the W end of Castle Eden Dene, where a small area was dominated by mature oaks.

To maintain a certain logicality in the description, the quarry site was numbered Site 1 and the oak woodland Site 9, though as will be shown below at least one other site could be considered as a starting point in the succession series.

1.2 Soil Sampling

Exhaustive sampling of the buried seed was not possible in the time available, but the sampling, begun early in May and completed by 15 May, had the advantage of restricting seeds to those species which accumulate buried seed rather than to those which do not, thus providing a better measure of the size and composition of the persistent seed bank.

Essentially, the method used consisted of the collection of 60 soil samples from each site, each one approximately 7 cm in



Map 3 SAMPLING SITE AT CASTLE EDEN DENE

OW Oak Woodland

scale : 0 50m

O.S. map 1:10 560 NZ43NW

diameter and 5 cm in depth, using a trowel to obtain the samples in the fashion outlined by Thompson and Grimes (1979). A 30 m tape was strung across a typical section of each site. Using this as the base line the soil samples were taken at co-ordinates randomly determined, 20 in each 10 metre square.

Within 48 hours of collection, the soil from each site was sieved through a 0.75 cm mesh to remove stones, twigs and roots. It was then consolidated and thoroughly mixed. One quarter of the soil was laid aside for soil tests and the remainder was placed in 5 seedling trays, 22 x 34 cm. These trays were prepared by lining with paper to prevent the accidental loss of seed through drainage holes, and a 0.5 cm layer of river gravel was placed on the bottom of the lined tray. Sieved soil (2 cm deep) was placed on top and kept sufficiently moist by tap water from above. Five replicates were made for each site. A control tray, filled with gravel and subjected to the same watering regime as the soil-filled trays, monitored the germination of any wind or water-borne seed present in the greenhouse. The 46 trays were placed on benches in an unheated greenhouse with a natural day-length/light regime.

Within 2 weeks several seedlings appeared. Identification presented some problems. Chancellor's 'Guide to Weed Seedlings' (Chancellor 1966) was helpful; but, in many cases, similar seedlings were grouped together and a few from each group transplanted into Arthur Bayles potting compost and grown until they flowered and could be identified more easily. Biennial plants were identified on vegetative characteristics (Clapham, Tutin and Warburg 1962). After 6 weeks the first crop of seedlings were removed to reduce overcrowding and competition. To encourage germination of as many as possible of the seeds present, the soil was then stirred and the process repeated. All seedlings which appeared by 15 August 1978 were counted and identified. The results of these germination tests are recorded in Appendix 1 where seedling species are listed alphabetically and in Appendix 2 where the details of each site and each replicate tray are given.

1.3 Vegetation Survey

The ground flora was recorded using one hundred 10 cm^2 quadrats, randomly selected at each site and the presence of each species in the quadrat noted. Plants occurring on the site, but not recorded within the 100 quadrats were also noted. The vegetation survey was made in June and early July when the appearance of flowering heads made the identification of grasses easier, but resulted in an under-representation of early flowering species (eg) Anemone nemorosa, Primula veris and some later flowering plants (e.g) Campanula rotundifolia. The ground flora for each site is recorded in Appendix 3 and the plant nomenclature is taken from 'Flora of the British Isles' (Clapham, Tutin and Warburg, 1962).

1.4 Description of each sampling site

Site 1 : Wingate Old Quarry (NE 373373)

Within this abandoned quarry a relatively flat, well-drained site at the base of a bank 2 m high was selected. Photo 1a The level part was about 100 m long, but varied in width from less than 10 m to about 60 m. It was traversed by several footpaths, so the sampling points were taken from the narrower E end to avoid clearly distinguishable paths; though it is to be regarded as a site subjected to some trampling. Each of the sites in the series had at least one footpath passing through or nearby; selection in each case was made so to collect soil from the least disturbed area, and so the Quarry had no unusual features in this respect. What clearly distinguished it was the pale, thin mineral soil, quickly subject to droughting. Nevertheless the ground surface was almost completely covered with vegetation, and only 3 quadrats had no vegetation present. Apart from Site 4, the Ungrazed Grassland, this was the most species-rich site with Lotus corniculatus as the dominant species. Agrostis stolonifera was the most common of the grasses, but Festuca ovina and Briza media were well represented. Carex flacca occurred in one third of the quadrats. Locally clumps of Trifolium spp. occurred, but shrub species, eg Crataegus monogyna and Rosa spp., although present in other older parts of the quarry, did not occur in the area sampled.

Site 2 : Arable Field

When the soil was collected from this site on 4 May the field of about 10 ha. at the foot of the wooded slope, had every appearance of the American-type One Year Old-Field. Neighbouring arable fields had been ploughed and drilled, though in none was there any sign of germinating crops as the spring had been cold and late. One the evening following the soil sampling session, the stubble in the sample field was burnt and ploughing began the next day. Thus the seedlings recorded are from seed buried in the soil prior to sowing the cereal crop, whereas the vegetation survey, made in June, included growing plants of Hordeum vulgare. In addition to this Chenopodium album, a common arable weed, was found in 90% of the quadrats. Stellaria media occurred in a few quadrats. Sinapis arvensis and Sonchus arvensis were present. The vegetation survey of this site is probably the least adequate of any, due to the inexperience of the recorder in recognizing newly germinated seedlings and the impossibility of making the survey later.

It was known that until 2 years ago this field had been part of the ungrazed grassland which constitutes Site 4 (J.P. Doody - personal communication). The photograph (Plate 1) shows the close proximity of Sites 2 and 4. In a survey carried out c.1950 (Heslop-Harrison and Richardson 1952) 71 species were recorded in this 'rough pasture' of Cassop Vale. Thus the present study provides an opportunity to assess the impact of recent cultivation on the buried seed population in species-rich calcereous grassland.

Site 3 : Grazed Grassland

This field was adjacent to Site 2 (Plate 2) occupying a similar break in slope at the foot of the wooded ridge. The soil samples showed that this site had a similar stony soil but, as it was grass covered, it was not apparent to the eye as in Site 2. Grasses, including *Lolium perenne*, *Holcus lanatus* and *Dactylis glomerata*, were well represented but *Trifolium pratense* and *Trifolium repens* were dominant. The presence of large numbers of *Lolium perenne* and *Trifolium pratense* indicated that the field had been sown. Disturbance remained a feature of this site as it was used for grazing by beef cattle, but it was not high quality pasture and locally thistles, *Cirsium arvense* and *Cirsium vulgare*, were invading the grassland.

Site 4 : Ungrazed Grassland

This site occupied a small area of about 20 x 20 m on the slope above Site 2, the Arable Field and was surrounded by hawthorn scrub which was invading it. (Plate 1). It showed the richness of species typical of calcereous grassland. Poterium sanguisorba 68% was the most common species, followed by Centaurea scabiosa 40% and Carex flacca 40%.Sieglingia decumbens 30% was the most common grass though 10 other grass species were present, including Festuca rubra 26% Briza media 24% and Bromus erecta 24%.

This open, undisturbed habitat occupied a critical position in the succession series. It is threatened by the plough which rejuvenates the succession and by the natural processes of succession indicated by the invasion of hawthorn scrub.

Site 5 : Gorse Scrub

This site was located at the E end of the wooded side of the valley. (Plate 2). Soil samples and ground cover were recorded from an area which had been burnt during the late autumn of 1977. At the end of April 1978, the area was characterized by the blackened remains of Ulex europaeus and patches of bare soil, with a bright spring showing of Primula veris, Viola riviniana, V. reichenbachiana and Orchis mascula. By 4 July the ground was covered with a large variety of plants. Centaurea scabiosa 27% and C. nigra 24% with Ulex europaeus 24% were the most frequently recorded species, but there was nothing approaching the dominant species which characterized some other site (eg Lotus corniculatus 96% at the Quarry).

Site 6 : Hawthorn Scrub

This area lay to the west and adjacent to the Gorse Scrub. (Plate 1). The Crataegus monogyna was remarkably uniform: individual shrubs were 4-6 m high and spaced at intervals of 2-3 m apart. There was a considerable reduction in light in the scrub, even before bud-burst, compared with the grassland sites. The slopes were relatively unstable and there was evidence of former quarrying and current animal burrowing activity. This instability did not seem to affect the hawthorn which consolidated the dark brown soil. Sanicula europaea was the most commonly found species with Chaerophyllum temulentum, another umbellifer, well represented. Two species of grasses were found: Poa trivialis and Brachypodium sylvaticum, but their occurrence was patchy.

Site 7 : Ash with Hawthorn

On the W end of the S facing ridge, where the slopes are steeper, Fraxinus excelsior occurred with C. monogyna (Plate 3). The ash was 7 to 10 m high, spaced every 5-7 m, the hawthorn, 4-6 m high spaced every 2-3 m as at Site 6. The ash was regenerating naturally and the crown of the ash reached several metres above the hawthorn, but the upper part of the hawthorn was in flower before the ash had any leaves. Despite the greater angle, the slopes appear to be more stable, and are covered with a lusher vegetation. Poa trivialis and Geum urbanum were found in 50% of the quadrats and Chaerophyllum temulentum in 40%. Locally Urtica dioica was abundant, a fact which suggests an additional source of nutrients, and Galium aparine was fairly common throughout. The other 11 species were found in less then 8% of the quadrats.

Site 8 : Ash with Sycamore

This site was on the N facing slope of Cassop Vale where the tree canopy was virtually complete with ash 13-15 m high as the dominant tree, but mixed with sycamore of 10 m high. (Plate 4). The shrub layer of Coryllus avellana 4 m high, which had been coppiced, and Crataegus monogyna 5-6 m, was much thinner than on the S facing slopes (Sites 6 and 7). Poa trivialis and Dactylis glomerata dominated the ground vegetation. The site was grazed by cattle (Plate 5). Those cattle, which had grazed elsewhere, may have carried seeds from improved grassland which were then deposited in their dung. Thus contributing to the store of buried seed in the Ash/Sycamore site. This point will be discussed later.

Site 9 : Oak Woodland

A group of 7 mature oaks distinguished this woodland from neighbouring areas of elm, beech and ash. They occurred on the upper part of a steep S facing slope at the W end of Castle Eden Dene (Map 3) in an area of approximately 30 x 30 m. The dark brown soil had a deep litter layer and was fairly easily disturbed. At the E end of the site and on the steeper slopes, there was evidence of some soil disturbance. Rubus fruticosus was most common at this end. Pteridium aquilinum was found mainly in the central portion where Arrhenatherum elatius was dominant. This is not a grass commonly associated with oak woodland, but it thrived at this site. Endymion non-scriptus (Plate 6) was common throughout the site. Though the litter was deep with rotting oak leaves and bracken fronds, more 'empty' quadrats, 5, were found here than on any other site. The robust nature of the bracken and the dense shade cast by its fronds, re-inforced the shade cast by the oaks. Anemone nemorosa and Endymion non-scriptus utilized the available light in the early part of the spring before the development of foliage by the oak and bracken.

1.5 Determination of the Age of the Sites

This presented some problems; at the woody sites the age of the dominant woody species was taken as the age of the site. (Table 1). These ages were determined approximately from documentary sources (O.S. Maps, Baker and Tate 1868, Heslop-Harrison and Temperley 1939, Heslop-Harrison and Richardson 1952). The age of sites earlier in the succession had been determined in some studies (Oosting and Humphrey 1940, Livingston and Allessio 1968) by reckoning the time since they were abandoned. The apparent ready availability of 'Old Fields' of different ages in the United States gives those studies a chronological tidiness which is not possible in Britain. It was relatively simple to find out that the Quarry had been abandoned 15 years but, as this time is probably not sufficient for a seed bank to develop which is in equilibrium with the vegetation, the Quarry retains many characteristics of an early successional site. In contrast, at the Grazed and Ungrazed Grassland sites, the seed bank is almost certainly in equilibrium with the vegetation; even though it is probably less than 15 years since the Grazed Grassland site was re-seeded with such species as Lolium perenne and Trifolium pratense. It may be assumed that these sites are 'older' than the Quarry.

The Arable Field, which has a 'successional' age of zero, was ploughed for the first time 2 years ago. One would expect that this is not sufficient time for the seed bank to reach its equilibrium size. Compared with other studies (Brenchley and Warington 1933, Champness and Morris 1948, Chippendale and Milton 1934) in which seeds in arable fields reached high numbers (29,000/m^2) relatively few seeds (1977/m^2) were obtained from the arable field site in this study. Thus the Arable Field had characteristics of an early successional site.

In this study then, there are two starting points for the successional series: the Quarry, which is an example of re-colonization from bare rock, and the Arable Field, which was formerly Ungrazed Grassland. In neither of these sites is the seed bank in equilibrium with the vegetation. Whereas, on all other sites it is assumed that there has been sufficient time for this equilibrium to have occurred and the series proceeds through Grazed and Ungrazed Grassland, Gorse Scrub, Hawthorn Scrub, Ash with Hawthorn, Ash/Sycamore and is completed with Oak Woodland.

Table 1 : SUMMARY OF RESULTS

Key	Sites	Age in yr.	pH	Seedlings Total	Seedlings /m²	Seedlings Nos. of Species	No. of species in vegetation
Q	Quarry	15	7.8	786	4537	20	48
AF	Arable field	1	7.6	342	1977	23	6
GG	Grazed Grassland	?	7.4	970	5607	24	36
UG	Ungrazed Grassland	?	7.6	275	1589	30	55
GS	Gorse Scrub	?	7.6	212	1225	25	38
HS	Hawthorn Scrub	50+	7.5	132	763	21	23
AH	Ash/ Hawthorn	80+	7.4	269	1555	14	22
AS	Ash/ Sycamore	100+	7.5	553	3179	14	21
OW	Oak Woodland	150	5.2	20	116	6	12

CHAPTER II : RESULTS OF GERMINATION TESTS

2.1 Total across the Successional Series

2.1 (a) General Trends

The total number of seedlings which emerged was 3556. Of these 28 were unidentifiable as they had not exhibited recognizable characteristics by the time the experiment ceased on 14 August 1978. Some could be identified only to the family (eg) several compositae. The same plant nomenclature was used as for the ground vegetation (Clapham, Tutin and Warburg 1962). The details of the germination tests at each site are recorded in Appendix 1 and 2 and those of the ground vegetation in Appendix 3.

There was a considerable variation in the number of seedlings germinating at each site (Table 1 Plates 7-11). The highest numbers were recorded in the Grazed Grassland (970) and the Quarry (786). On these sites grasses accounted for most of the seedlings: 81.5% of the seedlings in the Quarry site were of Agrostis stolonifera and 46.08% of the seedlings in the Grazed Grassland were of Holcus lanatus and Poa trivialis.

After the peak in the Grazed Grassland, the numbers germinating declined progressively in the Ungrazed Grassland (276), Gorse Scrub (212) and Hawthorn Scrub (132), but the Ash/Hawthorn site (269) showed an increase which continued in the Ash/Sycamore (550), followed by a marked decline in the Oak Woodland to 20.

Keeping in mind the problems of distinguishing between chronological and successional age and the two possible starting points for the successional series, the sequence of sites recorded in the tables and figures follows an age sequence from the Quarry and Arable Field; the 'youngest', to the Oak Woodland, the 'oldest'. Results show no simple correlation of age with number of seedlings (Table 1, Fig.1) but, testing this relationship statistically, $r_s = -0.616$ which is significant at $P = 0.05$ level (Siegel 1956). Reasons for this relationship will be discussed later.

2.1 (b) Comparison with other studies

The depth of soil sampled was sufficient to include the bulk of the viable buried seed, (Chippendale and Milton 1934, Moore and Wein 1977) and the incubation period long enough to allow the appearance of most of the spring and summer germinating species. Despite the problems of obtaining an accurate assessment (Thompson 1977) it was felt that the number of seedlings per m^2 could be calculated, thus giving some figures which could be compared with other studies on buried seeds. (Thompson 1978 gives a convenient summary). As the soil samples in this study were collected early in May, autumn germinating species (see Chapter IV) were excluded and the total numbers/m^2 are probably a conservative estimate (Table 1).

Numbers in the early successional stages, 1977/m^2 for the Arable Field (barley), were low compared with 29,000/m^2 in the barley field at Woburn (Brenchley and Warington 1933) and probably indicates a lack of equilibrium between the number of seeds and the vegetation in the Cassop site which had so recently been converted from ungrazed grassland.
If Table 1 gives a low estimate of total numbers, the total for the Grazed Grassland, 5607/m^2 may have greater affinity to the 6909/m^2 for rundown pasture in Stratford-on-Avon (Milton 1943) than to the 5369/m^2 for good lowland rye pasture (Champness and Morris 1948).

Early successional stages in several American studies show great variation in numbers, though the numbers for Co. Durham are nearer those of Livingston and Allessio (1968) for Massachusetts than of Oosting and Humphreys (1940) for North Carolina. Areas dominated by trees give a wide variety of results in North America, but those of the Ash/Hawthorn and Ash/Sycamore sites lie within their range. The extremely low numbers for the Oak Woodland $116/m^2$ is lower than any recorded for forests, though the later stages of many successions are characterized by a marked drop in germinations (Livingston and Allessio 1968, Oosting and Humphreys 1940, Strickler and Edgerton 1976). These studies contain no site comparable to that at Old Wingate Quarry.

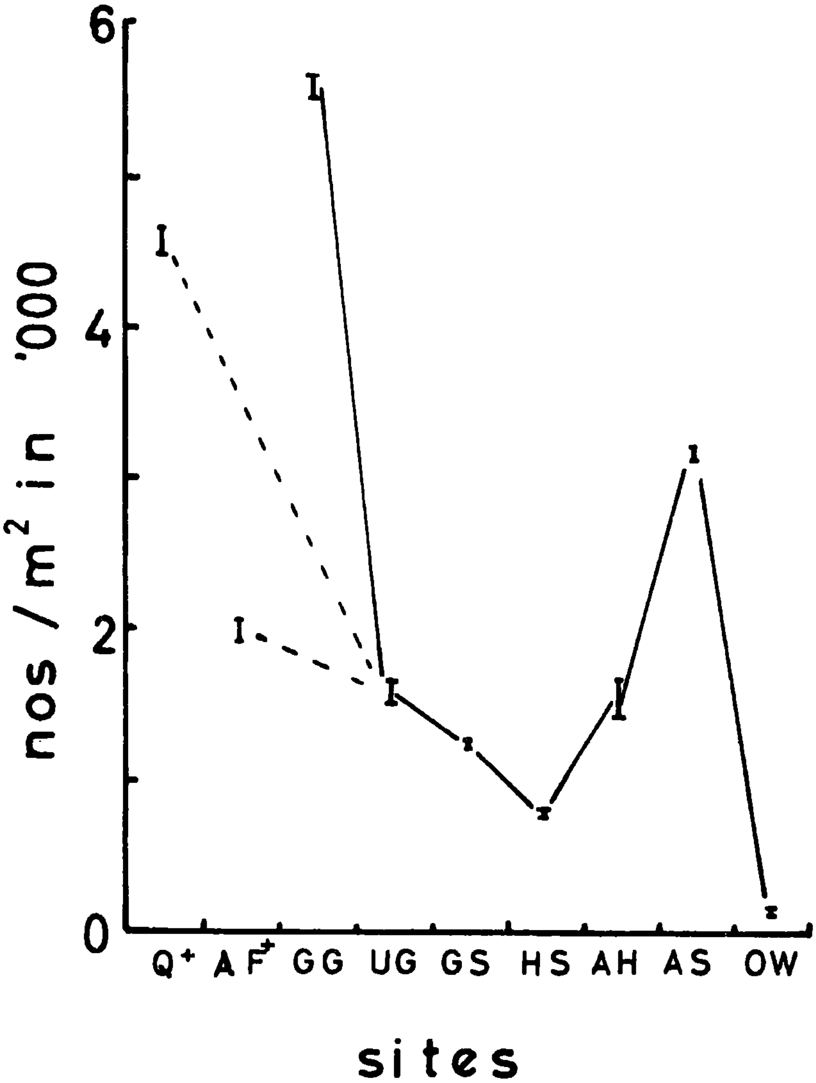
Though the number of seedlings fails to give a strict comparison, the densities obtained lie within the range of those obtained in studies for similar sites. The present study confirms the trend towards a decrease in total numbers in the older successional sites.

2.2 Seedling Species across the Series

The named seedlings represented 71 species. There was an increase in the number of species to a peak of 30 in the Ungrazed Grassland, followed by a decrease to the lowest number, 6, for the Oak Woodland. (Fig.2). A similar trend was noted in the Old Field successional series, though the Magnesian Limestone was less species-rich compared with the Piedmont Series in North Carolina, 127 species, (Oosting and Humphreys 1940) and more species-rich than the Harvard Forest, Massachusetts, 65 species. (Livingston and Allessio 1968).

The variation in the number of species of seedlings was not as great as that in the vegetation cover (Fig.2). There were 58 species

Fig 1 SEEDLINGS PER SQ. METRE



+ seedbank not in equilibrium with the vegetation

I average ± 1 S.E.

Fig 2   SEEDLING SPECIES & NUMBERS

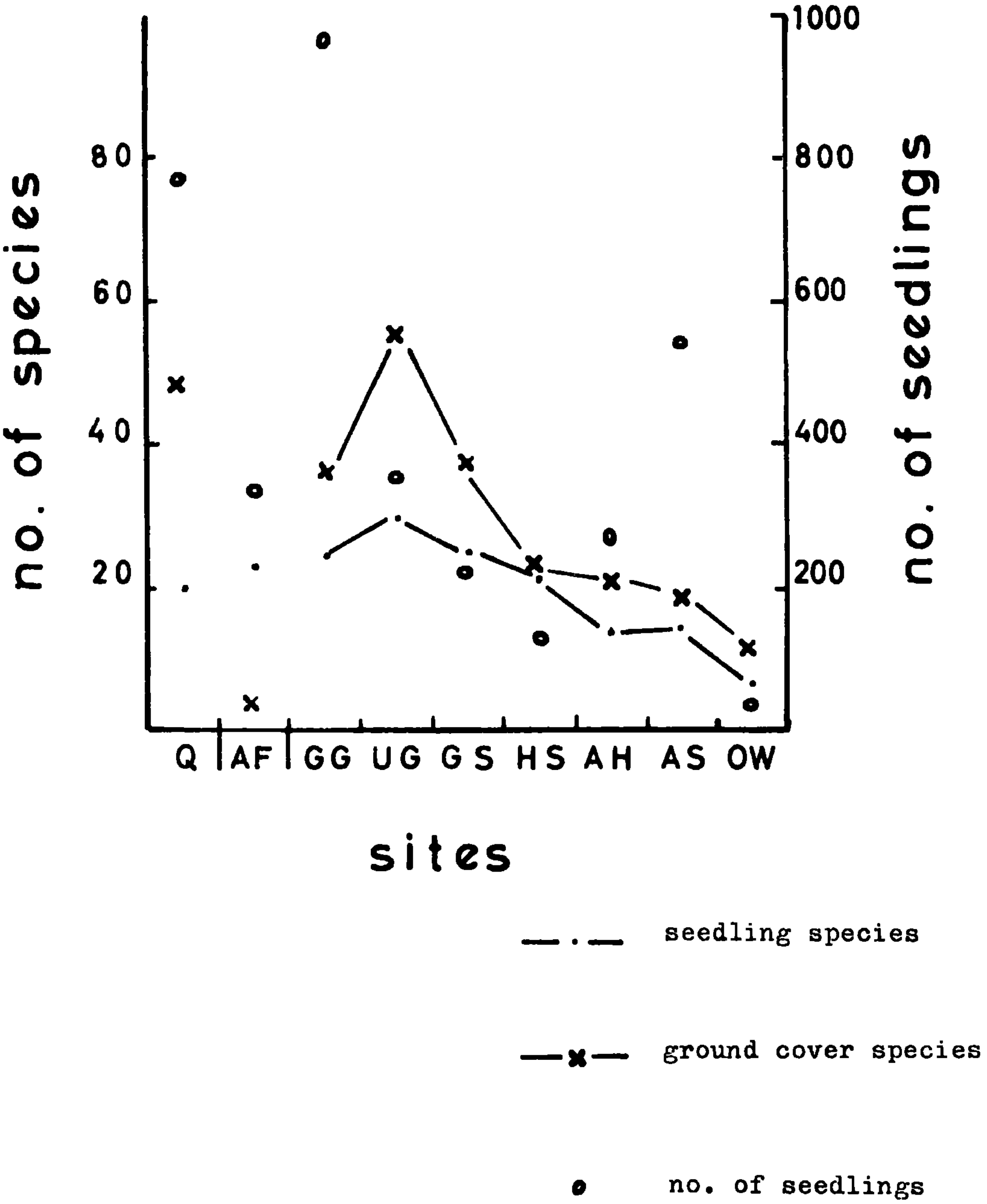


Fig 3 SEEDLING SPECIES COMMON TO SEVERAL SITES

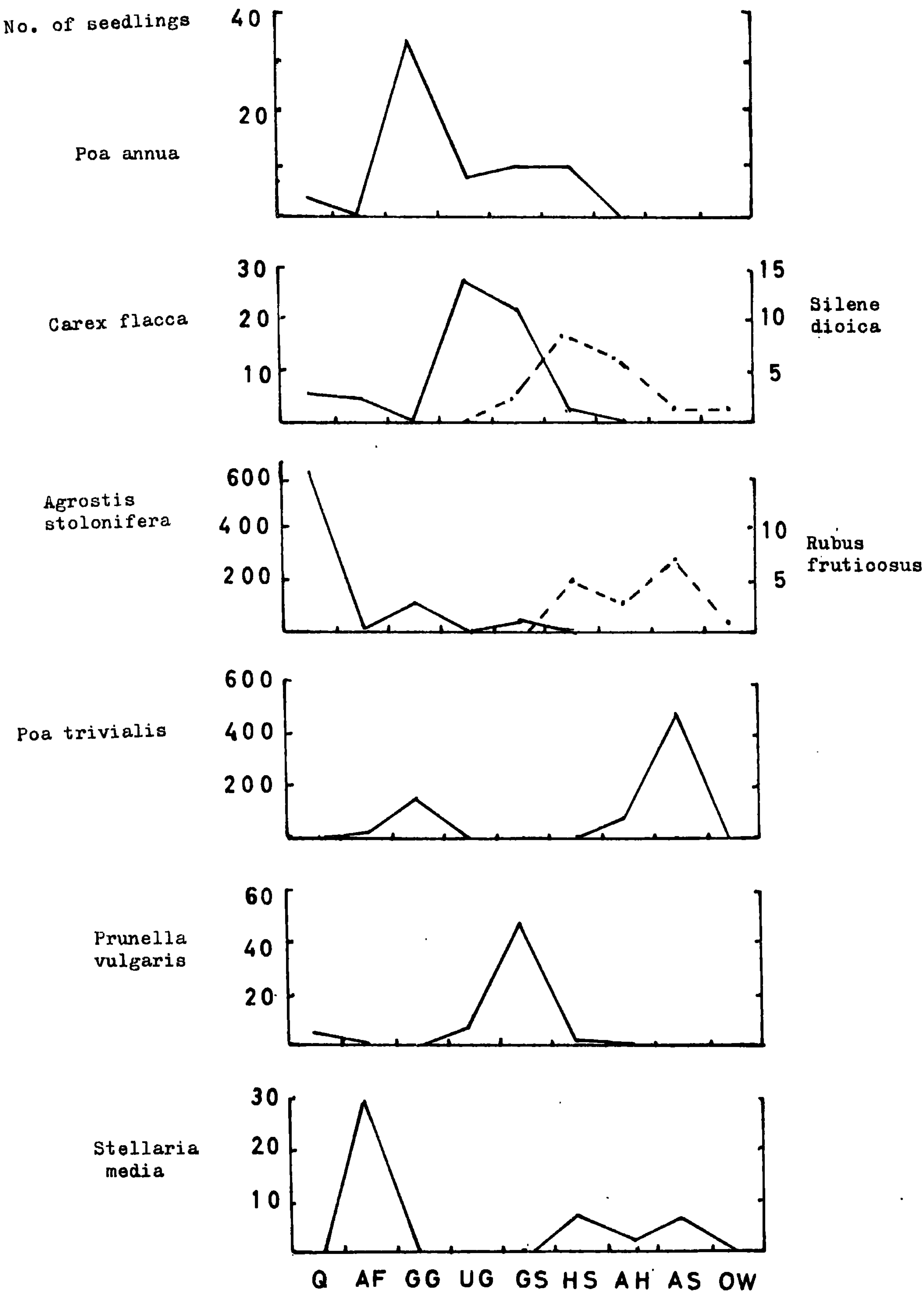
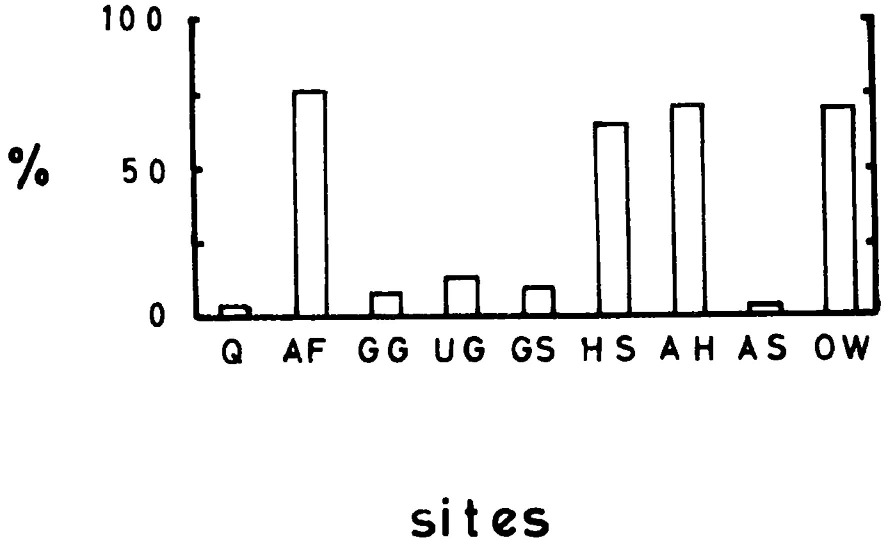


Fig 4 SEEDLINGS OF ANNUAL SPECIES



present in the ground cover which were not recovered among the seedlings and there were 16 seedling species which did not occur in the vegetation at that particular site.

No species occurred at every site, unlike the findings of Livingston and Allessio (1968). If single occurrences are excluded, then 2 species were found in 5 sites: Carex flacca and Poa annua, both of them in the early to middle stages of the succession. Fig. 3 shows the distribution of species common to several sites. Agrostis stolonifera and Prunella vulgaris have similar distributions to C. flacca and P. annua. The later stages of the succession are represented by Rubus fruticosus and Silene dioica. Poa trivialis and Stellaria media are present in both early and late stages, but are absent from the middle section. Thus, there is no simple sequence of plant species replacing each other in an ordered fashion across the succession as found in some of the classical studies (Cowles 1901).

The Arable Field contained 68.5% of the species of seedlings across the series. Many of these species were annuals. Large numbers of seedlings of Moehringia trinervia which is an annual, occurred in the samples from the Hawthorn Scrub and the Ash/Hawthorn sites, but relatively few perennial seedlings were obtained. Seedlings of the woody perennial species, which figured conspicuously in the ground cover, eg. Sanicula europaea were completely absent. The high percentage of annual species among the seedlings in the Oak Woodland (Fig. 4) was more apparent than real: 11 of the 20 seedlings were Polygonum aviculare, possibly brought in by birds. But at this site the dearth of seedlings was more significant than the percentage of annual species. Unlike the studies of Livingston and Allessio (1968) and Oosting and Humphreys (1940), the buried seeds gave no evidence of the former vegetational history of this site where the dominant vegetation has been established for much longer than seeds are likely to survive.

In general the proportion of annual species declined after the Arable Field, though an increase in the Hawthorn Scrub and Ash/Hawthorn sites is to be noted, but possible explanation is reserved for discussion later. Apart from the lack of evidence of the past vegetational history of the sites, the species pattern was similar to that obtained in other successional studies. The number of seedlings, their distribution across the series, and the number of species indicated that a loose successional series does in fact occur across the sites selected.

2.3 Results from Individual Sites

Quarry

More than 80% of the seedlings were *Agrostis stolonifera*. The other 19% were spread over 19 species. This site has few equivalents in other successional studies as it represented the colonization of mineral soil developed on quarry waste, but the lack of equilibrium between the seed bank and the vegetation cover, after 15 years freedom from disturbance, emphasizes how slowly a persistent seed bank builds up, even in the relatively receptive parent material of the Magnesian Limestone.

Arable Field

This seedling population was dominated by *Chenopodium album*. Two other annuals, *Stellaria media* and *Sonchus asper*, were the next most numerous species and all three are common arable weeds. 23 species of seedlings were identified including the 6 species recorded in the vegetation cover. This is probably a considerable under-estimate of the species in the vegetation cover, but the survey was carried out when the sown barley crop was at seedling stage. Chenopodium album was much in evidence, but other species were not sufficiently developed to be recognized then and the growing crop prevented a later survey. The growth of a modern strain of barley, bred for synchronous seeding, combined with efficient harvesting methods, removed almost all of the large numbers of barley seed which must have been produced the previous year, so that very few (3) seedlings of Hordeum vulgare germinated in the trays of soil collected before the field was drilled this year.

Grazed Grassland

This gave rise to the highest number of seedlings (970) obtained from any one site. Hol~~ens~~cus lanatus, Poa trivialis and Cirsium arvense were the 3 commonest, accounting for 59.9% of the germinations. As will be discussed in more detail later, H. lanatus and P. trivialis have been recognized as grasses with persistent seed banks (Thompson and Grime 1979). Whereas Lolium perenne, with a transient seed bank, contributed only 1.27% of the seedlings, though it was present in 48% of the quadrats of the vegetation survey.

Ungrazed Grassland

Unlike the Quarry site the two most common species here, Sieglingia decumbens and Carex flacca, accounted for only 33% of the total seedlings. It was the most species-rich site for both seedling and vegetation, though there was a decline in the total number of seedlings produced compared with the 3 sites above.

Gorse Scrub and Hawthorn Scrub

The total number of seedlings continued to decline across these two sites. Most of the species found in the Gorse Scrub occurred earlier in the series. In some ways this site represents a transition between the open sites and the shaded woodland sites. The gorse probably indicates an environment subjected to periodic burning which creates a more open habitat.

10 species of seedlings not found in the earlier successional sites appeared in the Hawthorn Scrub site, though, as mentioned above, many species common in the vegetation did not occur among the seedlings.

Ash with Hawthorn

While there was a drop in the number of species represented in the seedlings (14), there was an increase in the total number of seedlings (269). Moehringia trinervia was the commonest species, accounting for 42%, followed by Poa trivialis, 29%. Eleven species contributed only 8.2% of the total seedlings at the site. All of the seedlings which appeared here also occurred at other sites.

Ash/Sycamore

This site, with a much more open canopy than the ashwoods on the other side of Cassop Vale, had the same number of species, 14, as the Ash/Hawthorn site, but has more than twice the total number of seedlings (550). Poa trivialis accounts for 87% of them.

P. trivialis also occurs in large numbers in the Grazed Grassland and as the Ash/Sycamore site was grazed by cattle, the possibility of an import of seed via the cow dung was considered. Also, the presence of Urtica dioica strongly suggests the addition of nutrients from somewhere and the dung of grazing cattle seems the most likely source. Although the evidence seems to point to this conclusion there is nothing equivalent to the range of species found by Dore and Raymond (1942) in their investigation into the viable seed in cow manure; but there is evidence that grazing cattle do supplement the store of buried seeds and that P. trivialis is one of the species whose seeds are able to survive the process of mastication, digestion and voiding.

Though P. trivialis and Urtica dioica made a large contribution to the seedling in the Ash/Hawthorn site, there was no evidence of cattle grazing. However, it was evident that some of the former quarry workings on the N side of Cassop Vale had been used as a rubbish dump for unwanted farm products (eg. straw) and it is conceivable that the remains of the muck-spreading tank may have been dumped at the top of the Ash/Hawthorn ridge, thus affecting the vegetation down part of that slope and accounting for the local abundance of Urtica dioica in the vegetation cover.

The one tree-species seedling obtained was Betula spp. and this occurred at the Ash/Sycamore site. It is known that Betula produces many seeds which are easily dispersed. Natural regeneration of Ash, and more particularly Sycamore was evident, but no seedling of either species appeared in the germination tests.

Oak Woodland

The seedlings which germinated were few in number and in species. Though the soil sieving process would eliminate large seeds, in fact there were no acorns in the soil samples, nor is any regeneration of the oak apparent. Endymion non-scriptus and Arrhenatherum elatius were abundant in the vegetation, but produced no seedlings. Those few seedlings which did occur, appeared also earlier in the successional series, though many had probably been brought to the site by birds. There is no evidence that this site has ever been anything other than oak woodland during the last 150 to 200 years.

2.4 Summary

Before discussing some of the processes which might underlie these facts, the evidence presented above seems to indicate the following findings:

1. The distribution in terms of numbers of both species and individuals is similar to that found in studies of other successional series (Livingston and Allessio 1968, Oosting and Humphreys 1940). Consequently the experimental sites, ordered roughly as above, may be assumed to represent a successional sequence.

2. The total number of seedlings germinating reached a peak early in the series and then decreased across the older sites.

3. The total number of species of both seedlings and ground vegetation showed similar trends, though there was less variation in the seedlings than in the vegetation.

4. A large number of early successional seedlings were annuals.

5. Seedlings of most species typical of woodland vegetation and all tree species were absent.

CHAPTER III : DISCUSSION I : MECHANISMS OF SUCCESSION

3.1 Introduction

Disturbance is a fundamental factor in succession, and the period since the last disturbance is a common gradient on which succession has been measured. (Livingston and Allessio 1968, Auclair and Goff 1971, Shafti and Yarranton 1973). Species which can exploit the environment created by disturbance, 'opportunists' (Colinvaux 1973), give way gradually to those which can tolerate shade and the depletion of mineral nutrients which occurs in the later successional stages (Crocker and Major 1955). The analysis of these parallel and opposing gradients of disturbance and stress (Thompson 1978) has been approached in different ways depending on whether the mechanism of succession has been diagnosed as residing in individual species or in the community as a whole.

3.2 Species Diversity Across the Successional Sequence

Along the continuum from early to late stages, groups of species have been regarded as constituting distinct communities. The diversity of these species has been taken as a measure of the organization of each community. (Margalef 1969, Odum 1969). Animal ecologists have found that an increase in species diversity occurs as the succession proceeds (Williams 1964). Plant ecologists have not always found the same feature, though some increase in species diversity across the series is a feature of most successions. When the number of species of seedlings and the number of species in the ground vegetation for each site is graphed, (Fig.2) both curves reach a peak with the Ungrazed Grassland, and then progressively decline through the woody sites. There is less variation between the sites in the seedling species than in the vegetation species. In every case there are fewer seedlings species than vegetation species, with the exception of the Arable Field where, as mentioned above, the vegetation survey probably under-estimates the number of species. These curves are similar to those of Livingston and Allessio (1965), Auclair and Goff (1971), but are unlike those of Nicholson and Monk (1974) where, in an old field - forest succession, the number of species reached the highest value early in the series and remained constant throughout the rest of the series. Though the findings here do indicate that seedlings show a similar species diversity to plant communities, this diversity gives little indication of the mechanics of succession. A consideration of the forces affecting individual plants might be more fruitful.

3.3 Impact of Primary Growth Strategies

Basically it must be agreed that 'a satisfactory explanation of succession must be compatible with the theory of evolution by natural selection' (Colinvaux 1973). The importance of genotypic variation and phenotypic response is widely recognized (Bradshaw 1959, Harper and Ogden 1970) but, in considering the nature of succession, a model which incorporates environmental variation and plant types is more helpful. Grime (1977) considers that the two external factors limiting plant biomass are disturbance, which he defines as that which damages or destroys the plant itself, (eg.) fire, herbivores, soil erosion, and stress defined as that which restricts plant productivity (eg.) suboptimal light, water, mineral nutrients. The environments are classified according to whether the stress is high or low and whether the disturbance is high or low, then 4 types of environment emerge:

Table 2 : CHARACTERISTICS OF PLANTS SHOWING PRIMARY STRATEGIES OF GROWTH (after Grime 1977)

Characteristic	Ruderal	Competitive	Stress-tolerant
1. Morphology of shoot	Small	Extensive	Varies widely
2. R_{max} (Maximum potential relative growth-rate)	Rapid	Rapid	Slow
3. Life form	Annual herbs	Perennial herbs, shrubs & trees	Perennial herbs, shrubs & trees
4. Proportion of annual production devoted to seeds	Large	Small	Small

1. Disturbance and stress high - in which no plants grow.
2. Disturbance high, stress low - in which ruderals grow.
3. Disturbance low, stress high - in which stress-tolerant plants grow.
4. Disturbance and stress low - in which competitive plants grow.

These 4 environmental types give rise to 3 primary strategies of growth: ruderal, competitive and stress tolerant. Table 2 lists 4 characteristics of species showing these primary strategies. Attempts have been made to classify vegetation by reference to these strategies (Grime 1974), (Grime and Hunt 1975) which may be regarded as extremes, whereas individual plant species represent a compromise between the selection pressures from stress, disturbance and intra- and inter-specific competition. Typically, trees and shrubs are stress tolerant, most ruderals are annual weeds, and perennial herbs range from ruderal to stress-tolerant, though many are competitive.

In the sites across the Magnesian Limestone, disturbance is high early in the succession in the Quarry and Arable Field and low in the wooded sites which close the series. Stress is low at the start of the series and increases as it progresses, when shade increases and mineral nutrients decrease. The pattern follows that of Fig.5. Thus, one might expect ruderal species to be early in the succession, competitive plants to dominate the central portion and stress-tolerant plants to complete the series. In accordance with this, annual weeds were found in the Arable Field (eg.) <u>Chenopodium album</u>, competitive species among the grassland sites eg. <u>Holcus lanatus</u> and shrubs and trees completed the series.

In order to obtain a more precise relationship between the three primary strategies and the results recorded in Appendix 1 and 2, an attempt was made to correlate the number of seedlings with the average R_{max} of the most numerous species in the vegetation cover at that site. This gave a weak positive correlation which, however, was not significant. The role of the three primary strategies therefore lacks precision in so far as this study can show. This is not entirely unexpected as these strategies refer specifically to mature plants. The juvenile stages with which this study is particularly concerned differ from the mature plant. Not only is the seedling most vulnerable, but it is also the most critical stage in the recruitment of new plants into a community by germination. It could be claimed that succession starts with the germination of seeds.

CHAPTER IV : DISCUSSION II : SEEDS, SEEDLINGS AND GERMINATION STRATEGIES

4.1 Introduction

Where conditions of moisture and temperature are suitable, germination can take place. But unless the newly germinated seedling can be established sufficiently to grow and develop, the mature plant will not be produced and the whole process will be a wasteful expenditure of energy. The establishment of healthy seedlings is crucial, and it is only in these terms that germination can be considered 'successful'. Rorison (1960) showed that seedlings sown on bare soil produced large healthy plants which flowered at the end of the first year, whereas those sown in turf were stunted and did not produce any flowers. This seems to indicate that enrichment is facilitated by low levels of competition. These low levels occur where there are gaps in the canopy (equivalent to Rorison's bare soil experiment) and in this way germination has come to be regulated by mechanisms which enable seeds to detect canopy gaps. The diurnal fluctuations in temperature and the presence or absence of light are stimuli for germination. Species have particular requirements for diurnal fluctuation in temperature. These requirements are related to those obtaining in habitats in which the species are found and this relation provides the mechanism which causes seeds to germinate at times and in places favourable for seedling establishment. (Thompson, Grime and Mason 1977).

4.2 Regeneration strategies

The successful detection of suitable gaps by particular species led Thompson (1977) to classify the occurrence of these gaps on the basis of predictability in both time and space, and to distinguish the associated disturbance into 'severe' or 'moderate'. From this he recognized several regeneration strategies and classified the plants in the following groups:

a. Ruderal and Competitive Adventives

'Opportunist' plants utilize gaps which can rarely be predicted in time or space. In Britain such disturbance is usually man-made. Plants which exploit these disturbed environments are to be found among the arable weeds. Ruderals (eg.) Senecio vulgaris, are usually annuals with a high R_{max} (Senecio Vulgaris $R_{max} = 1.63$) and produce a large number of wind-dispersed seeds, which are mobile and adapted to exploit newly disturbed habitats. Continuous disturbance is necessary for the ruderal adventives to persist. The competitive adventives produce a large number of wind-dispersed seeds, but they are perennials and, once established, are capable of persisting in an environment: (eg.) Chamaenerion angustifolium colonizes patches caused by burning, but persists also when the disturbance has ceased.

b. Ruderals with Seed Banks

Where the disturbance is severe, but is spatially or temporally predictable, for instance in arable fields, some ruderals eg. Chenopodium album produce seeds in large numbers, and accumulate buried seeds near to the parent plant ready to exploit the disturbance which occurs on a regular basis and which is necessary for successful establishment.

c. Species with Persistent Seed Banks

Where the disturbance is moderate, the gaps will be less frequent and less predictable. Many species in a variety of habitats accumulate a reservoir of germinable seed which is present throughout the year, ready to exploit the gaps whenever and wherever they occur. Seed banks have evolved as the optimum way of exploiting the small gaps occurring all the time in closed herbaceous vegetation. Species with seed banks include Campanula rotundifolia and Plantago lanceolata.

d. Species with Transient Seed Banks

Where gaps are highly predictable in time and space, some species have evolved a different strategy to exploit the expected gaps. These species include many grasses (eg.) Arrhenatherum elatius, Festuca rubra, Lolium perenne. They have relatively large seeds and no dispersal mechanism. Instead the germination of a single year's seed production takes place soon after the shedding of the seed. This synchronous seed germination is timed to coincide with a reduction in plant growth characteristic of many droughted habitats. Seeds shed in the summer germinate in the autumn. Seasonal grazing artificially creates similar conditions and grasses which are Mediterranean in origin are well adapted to grazed pastures. Seeds accumulate for a short period and germinate soon after shedding. The seed bank is absent during the rest of the year.

4.3 Seedling results and Germination Strategies

If the results of seedling germinations (Appendix 1 and 2) are examined in the light of these strategies, certain patterns become apparent. The nature of the experiment would lead one to expect that the species with persistent seed banks would be prominent among the seedling results. The 3 commonest species germinating at each site are, in virtually all cases, those with persistent seed banks eg. Agrostis stolonifera, Holcus lanatus, Poa trivialis. The major differences occur between the disturbed and the undisturbed sites.

4.3(a) Disturbed Sites

The principal component in the Arable Field is Chenopodium album, a common arable weed which is well adapted to regular disturbance by the production of a large number of seeds which accumulate near to the parent plant ready to exploit the predictable disturbance caused by ploughing. The Arable Field has the largest number of species of annual species (Fig.5).

Ruderals are much less evident in the vegetation of the Quarry site, but this site contains a mixture of species with persistent seed banks (eg. Agrostis stolonifera, Lotus corniculatus, Plantago lanceolata) and also species with transient seed banks adapted to germinate at the end of the summer drought (eg. Festuca ovina, Festuca rubra, Briza media). As would be expected from soil collected in the spring, the former group are well represented in the seedling numbers, whereas the latter are almost absent.

The Grazed Grassland site contained Lolium perenne which has a transient seed bank and is represented by very few seedlings, 1.2%. Most seedlings come from grasses which have permanent seed banks eg. Holcus lanatus, Poa trivialis and Agrostis stolonifera. In outward appearance Cirsium arvense might be regarded as belonging to the wind-dispersed ruderal adventive group which, as might be expected, is almost absent from this study of buried seed. There is evidence (Bakker 1960) that C. arvense is less easily dispersed by wind as it has a large seed which is easily detached from the papus, and this study shows that it is a species which accumulates buried seed.

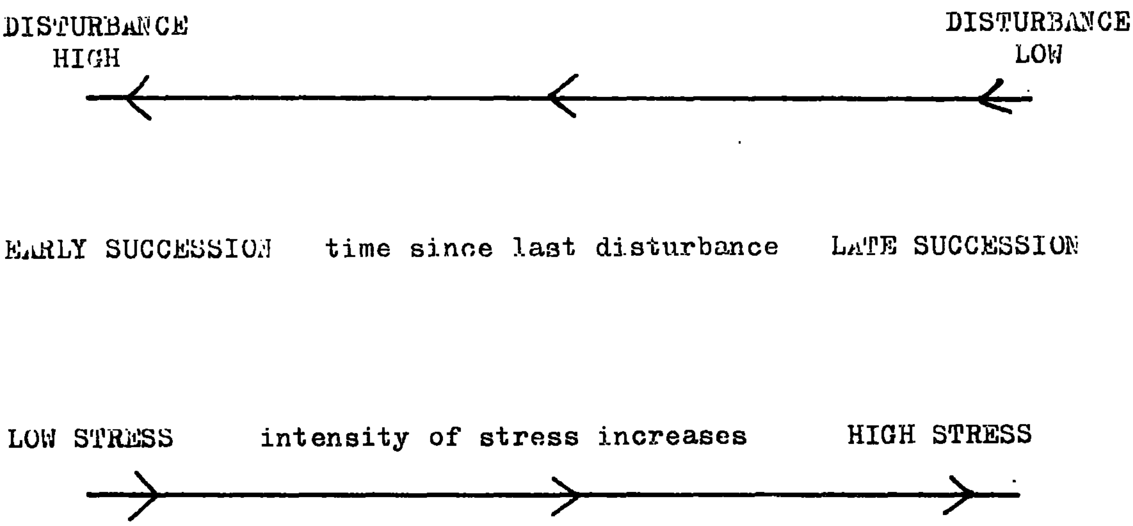
4.3(b) Undisturbed Sites

As the amount of disturbance decreases across the series, so the number of seedlings is reduced. This reduction may be related to a reduction in the species with persistent seed banks, which are associated with a lack of disturbance. The occurrence of large numbers of *Poa trivialis* seedlings in the Ash/Sycamore site, and, to a lesser extent on the Ash/Hawthorn site, is to be related to a local increase in disturbance. The slopes are unstable in the Ash/Hawthorn site and Cassop Vale is a fairly popular area for outdoor recreation which attracts dog-exercising walkers and adventure-seeking little boys. Some disturbance may be related to trampling. The Ash/Sycamore site is grazed, which would account for the increased disturbance and the *P. trivialis* seed bank may be supplemented by seeds deposited in the dung of grazing cattle.

The grass in the Oak Woodland site, *Arrhenatherum elatius*, has a transient seed bank, with germination occurring usually in the autumn, so one would not expect to find these seedlings in the germination tests. Of the annuals present *Polygonum aviculare* has a large seed which is eaten by pigeons and may have been introduced in this way. The top edge of the wood is close to an arable field which may have been the source of the *Chenopodium album* seedlings.

Buried seeds at all the undisturbed sites are relatively few in number. The vegetation is characterized by stress-tolerant species (eg.) *Sanicula europaea*. Tamm (1956) identified this plant as a very slow-growing species which flowers only intermittently. Grime and Jeffrey (1965) found that several species of common woodland plants were better able to survive in deep shade than were species which did not occur in woodlands. Hutchinson (1967) found that many woodland

Fig 5 DISTURBANCE AND STRESS ACROSS A SUCCESSION



species (eg.) Brachypodium sylvaticum and Deschampsia flexuosa were able to survive several months in complete darkness and able to return to normal growth in suitable light conditions. He suggests that it may be possible for these seedlings to germinate in favourable conditions, but then be able to persist in less favourable light conditions, ready to resume growth when more favourable conditions return. It would seem that in stressed habitats buried seeds do not accumulate, as this would be a wasteful expenditure of energy. Instead of buried seeds an alternative strategy may be recognized: a "seedling bank" where "seedlings are waiting for a chance". (Van der Pijl 1972).

4.4 The role of buried seeds in the gradients of stress and disturbance across a successional series

Thompson (1978) in examining theoretical considerations which influence the density and distribution of buried seeds, suggests that the accumulation of buried seed is favoured by high disturbance and low levels of stress. He cites a successional series as an example of "parallel and opposing gradients of stress and disturbance" along which disturbance decreases as succession proceeds, while stress increases (Fig. 5). From this he predicts certain characteristics of the buried seed along the series.

1. A fall in density of the buried seed from early to late succession;
2. Species typical of early successions persisting to mature forest, thus it may be difficult to obtain sites where the buried seeds are in equilibrium with the vegetation;
3. Seeds of tree species are absent;
4. Seed production in herb and shrub species is limited by shade and low nutrients;

5. Continuity during unfavourable periods is provided by mature plants in perennials but by seeds in annuals.

If germination is taken as an indication of the number of buried seeds then this study shows a fall in density of the seed across the series. The quarry and arable field sites are exceptions in that the number of seeds is probably not in equilibrium with the vegetation and additional disturbance in the Ash/Hawthorn, and Ash/Sycamore sites arrests the normal process of succession.

Some of the species present in the early succession persisted to the wooded sites (Fig. 3) (eg.) Poa annua, Agrostis stolonifera, but none persisted to mature forest. Seeds of the dominant tree species were absent.

Seed production of herbs and shrubby species declined in shady sites which are usually regarded as low in nutrients. Where there was an additional source of nutrients as at the Ash/Sycamore site, Poa trivialis flourished. Perennials were most common in those sites subjected to prolonged periods of shade and reduced nutrients, whereas annuals which produced large numbers of buried seed, occurred in disturbed, unstressed sites.

This study of a successional series in England appears to be in agreement with the predictions outlined above which also fit the American studies of Livingston and Allessio (1968) and Oosting and Humphreys (1940).

4.5 Application to aspects of Conservation

This study has to a large extent confirmed the suggestion that the density and distribution of buried seed is related to degrees of disturbance and levels of stress. Satisfying as it may be to find confirmation of such theoretical principles, some may question whether such studies have any relevance to major ecological problems.

Many ecologists concerned with the practical aspects of conservation have intuitively argued for policies of preservation at a time when the scale and rate of man-induced change to the natural environment is accelerating. The arable field in this study was, until 2 years ago, part of the species-rich ungrazed grassland, with, presumably, a seed bank similar to that of the ungrazed grassland site. As a result of ploughing, very few seeds remain which are typical of the ungrazed grassland; most are the typical arable weeds. It is difficult to re-establish pasture species, many of which have transient seed banks, whereas arable weed seeds persist for many years because of their permanent seed banks, (as seen in the Old-Field succession studies of Livingston and Allesio 1968, Oosting and Humphreys 1940).

It has been shown (Roberts and Dawkins 1967) that with regular disturbance over a 6 year period the number of viable weed seeds decreased exponentially and that the more frequent the disturbance the greater the reduction. The regular disturbance of agricultural activities, ploughing, harrowing and grazing, may be as destructive of many naturally occurring species in open grassland habitats as the intense disturbance of quarrying. In the Magnesium Limestone the species-rich calcereous grassland is an extremely fragile environment, readily destroyed by the plough, as it has been for centuries, and the earth moving machinery of the open-cast miner, which has appeared more recently. Of the two the plough is the more destructive. Soil stripping may preserve species while underlying rock is removed, but the regular disturbance of ploughing and grazing quickly destroys many species, replacing them by weeds. In order to conserve these species some patches of calcereous grassland must be left agriculturally unproductive.

The only ungrazed grassland which remained at Cassop was subject to natural invasion by hawthorn which, by the shade it casts, increases the stress and reduces the number of species. Such undisturbed sites are relatively few; their survival could be assisted by a form of management which would have to include ways of maintaining an open habitat in order to preserve a variety of species in the ground flora and in the seed bank.

Since the process of succession is dynamic the conservation of sites across a successional series will, therefore, involve those practices which mainly arrest the natural process of succession. In some cases this will require the prohibition of agricultural activity; in others the selective control of stress-inducing species.

Where descriptive studies, such as this, can be related to theoretical principles it may be possible to contribute to conservation based on sound ecological considerations.

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APPENDIX 1 : RESULTS OF GERMINATION TESTS

Seedling Species	Sampling Sites									
	Q	AF	GG	UG	GS	HS	AH	AS	OW	TOTAL
Agrostis stolonifera	641	5	103		32					781
Agrostis tenuis		1		4					3	8
Anagallis arvensis			15		4					19
Betula spp.								16		16
Brachypodium sylvaticum						3				
Campanula rotundifolia				4	2	2				8
Capsella bursa-pastoris					2					2
Carex flacca	6	5		27	23	3				64
Carex nigra				11						11
Catapodium rigidum				2	1					3
Cerastium fontanum		3	59							62
Chamaenerion angustifolium		3	3	2		1				9
Chenopodium album		250					1		3	254
Chrysanthemum leucanthemum	7			4						11
Cirsium arvense	2		134	6	1	1	2			146
Cirsium vulgare	1		4		1		1	1	1	9
Compositae spp.	9		1	6	6					19
Dactylis glomerata				19	3					22
Deschampsia caespitosa		2								2
Epilobium spp.	6				10		1			17
Epilobium hirsutum		2								2
Epilobium parviflorum						1				1
Festuca ovina				4	1					5
Festuca pratensis			53							53
Festuca rubra		3		16	1					20
Fragaria vesca					2	3	2			7
Geranium robertianum						2	2	2		6
Geum urbanum						2		2		4
Holcus lanatus	3	1	299	19	1					323
Hordeum vulgare		3								3
Hypericum perforatum					1					1
Juncus spp.				1				1		2
Juncus effusus		1								1
Juncus inflexus		3								3
Leontodon hispidus				5	8					13
Linum catharticum	5	1		19	2					27
Lolium perenne			12							12
Lotus corniculatus	41			3						44
Medicago lupulina	6									6
Moehringia trinervia						69	113			182
Ononis spinosa					26					26
Plantago lanceolata	9		1	9	3					22
Plantago media	1		14							15
Poa annua	4		34	7	9	9				63
Poa trivialis		5	148				78	480		711
Polygonum aviculare			5						11	16
Polygonum convolusus			1							1
Polygonum persicaria		1								1

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APPENDIX 1 (Cont'd)

Seedling Species	Sampling Sites									
	Q	AF	GG	UG	GS	HS	AH	AS	OW	TOTAL
Potentilla reptans	1		6							7
Poterium sanguisorba		1		7						8
Prunella vulgaris	5			6	48	2				61
Ranunculus repens			13	1			1	1		16
Rubus fruticosus						5	3	7	1	16
Rumex acetosa		3								3
Rumex crispus			18					1		19
Sagina procumbens	12									12
Sambucus nigra						2				2
Senecio vulgaris				1				1		2
Sieglingia decumbens				64	19					83
Silene dioica					2	8	6	1	1	18
Sinapis arvensis			5							5
Sonchus spp.	3							1		4
Sonchus arvensis			1			2				3
Sonchus asper		17		9	3		1			30
Sonchus oleraceous		1								1
Stachys sylvatica						3		2		5
Stellaria media		29				7	2	6		44
Succisa pratensis						1				1
Trifolium pratense	1			10						11
Trifolium repens	9		34	3						46
Tripleurospermum maritimum		1		1						2
Urtica dioica		1	1	1			54	30		87
Veronica chamaedrys						2				2
Viola odorata						3				3
Viola arvensis			1							1
Unidentified	14		5	4	1	1	2	1		28
TOTAL	786	342	970	275	212	132	269	553	20	3556

APPENDIX 2 : DETAILS OF SEEDLING SPECIES AT EACH SAMPLING SITE

QUARRY

Species	Trays 1	2	3	4	5	Total
Agrostis stolonifera	156	94	113	137	141	641
Lotus corniculatus	7	5	6	8	15	41
Sagina procumbens	3	3	1	2	3	12
Compositae sp. (unidentified)	4	2		3		9
Plantago lanceolata	2	2	2	2	1	9
Trifolium repens	8			1		9
Chrysanthemum leucanthemum		2		3	2	7
Carex flacca	1			3	2	6
Epilobium spp. (unidentified)	2	1	3			6
Medicago lupulina		2		2	2	6
Linum catharticum	4		1			5
Prunella vulgaris		3		1	1	5
Poa annua				2	2	4
Holcus lanatus			1	1	1	3
Sonchus sp.			1	1	1	3
Cirsium arvense				1	1	2
Cirsium vulgare		1				1
Plantago media					1	1
Potentilla reptans				1		1
Trifolium Pratense				1		1
Unidentified	1		3	3	7	14
Total no. of seedlings	188	115	131	172	179	786
Total no. of species	9	10	8	16	13	20

SEEDLINGS

ARABLE FIELD

Species	Trays 1	2	3	4	5	Total
Chenopodium album	47	54	54	41	54	250
Stellaria media	6	4	5	10	4	29
Sonchus asper	2	5	2	3	5	17
Agrostis stolonifera			2	2	1	5
Carex flacca	2	1		2		5
Poa trivialis	1		1	3		5
Cerastium fontanum	1			2		3
Chamaenerion angustifolium			1	2		3
Festuca rubra	1	2				3
Hordeum vulgare			2		1	3
Juncus inflexus	1	1	1			3
Rumex acetosa		2			1	3
Deschampsia caespitosa			2			2
Epilobium hirsutum				2		2
Agrostis tenuis	1					1
Holcus lanatus		1				1
Juncus effusus			1			1
Linum catharticum	1					1
Polygonium persicaria	1					1
Poterium sanguisorba	1					1
Sonchus oleraceous	1					1
Tripleurospermum maritimum	1					1
Urtica dioica					1	1
Total no. of seedlings	67	70	71	68	66	342
Total no. of species	14	8	9	9	7	23

SEEDLINGS — GRAZED GRASSLAND

Species	Trays 1	2	3	4	5	Total
Holcus lanatus	66	56	47	73	57	299
Poa trivialis	38	26	26	39	19	148
Cirsium arvense	28	30	27	27	22	134
Agrostis stolonifera	2	17	41	2	41	103
Cerastium fontanum	11	14	13	13	8	59
Festuca pratensis	11	10	10	12	10	53
Poa annua	5	6	6	9	8	34
Trifolium repens	11	2	2	10	9	34
Rumex crispus	2	5	2	5	4	18
Anagallis arvensis	2	2	3	5	3	15
Plantago media			4	7	3	14
Ranunculus repens	3	5	1	2	2	13
Lolium perenne	4	3	3	1	1	12
Potentilla reptans	2		1	2	1	6
Polygonum arviculare		2	1	1	1	5
Sinapis arvense	2	1	1		1	5
Cirsium vulgare			3	1		4
Chamaenerion angustifolium			3			3
Compositae spp.				1		1
Plantago lanceolata				1		1
Polygonum convolulus				1		1
Sonchus arvensis	1					1
Urtica dioica	1					1
Viola arvensis				1		1
Unidentified		3		1	1	5
Total no. of seedlings	189	182	194	214	191	970
Total no. of species	16	12	15	20	14	24

SEEDLINGS — UNGRAZED GRASSLAND

Species	Trays 1	2	3	4	5	Total
Sieglingia decumbens	7	18	14	10	15	64
Carex flacca	6	5	4	4	8	27
Dactylis glomerata	6	5	1		7	19
Holcus lanatus	3	4	3	2	7	19
Linum catharticum	4	2	3	5	5	19
Festuca rubra	2	5	4	1	4	16
Carex nigra	5		1	3	2	11
Trifolium pratense	3	3	3		1	10
Plantago lanceolata	1		4	1	3	9
Sonchus asper	1	4		1	3	9
Poa annua		1		6		7
Poterium sanguisorba	1		1	2	3	7
Cirsium arvense	1	3	2			6
Compositae	1	2		1	2	6
Prunella vulgaris	1	1	3	1		6
Leontodon hispidus	4		1			5
Agrostis tenuis	4					4
Campanula rotundifolia			2	1	1	4
Chrysanthemum leucanthemum		1			3	4
Festuca ovina	2				2	4
Lotus corniculatus	2	1				3
Trifolium repens	1	1	1			3
Catapodium rigidum		1	1			2
Chamaenerion angustifolium	1				1	2
Juncus sp.					1	1
Ranunculus repens	1					1
Senecio vulgaris				1		1
Tripleurospermum maritimum					1	1
Urtica dioica			1			1
Unidentified		3			1	4
Total no. of seedlings	57	61	49	39	70	275
Total no. of species	21	17	17	14	18	30

SEEDLINGS

GORSE SCRUB

Species	Trays 1	2	3	4	5	Total
Prunella vulgaris	7	10	9	14	8	48
Agrostis stolonifera	8	4	9	3	8	32
Ononis spinosa	2	1	6	7	10	26
Carex flacca	4	4	7	3	5	23
Sieglingia decumbens	2	2	7	4	4	19
Epilobium sp.	5	2	2	1		10
Poa annua	1	2	3	3		9
Leontodon hispidus			1	5	2	8
Compositae	4	2				6
Anagallis arvensis		2	1		1	4
Dactylis glomerata		2			1	3
Plantago lanceolata		1		2		3
Sonchus asper	3					3
Campanula rotundifolia		1	1			2
Capsella bursa-pastoris	2					2
Fragaria vesca	1	1				2
Linum catharticum					2	2
Silene dioica	1				1	2
Catapodium rigidum		1				1
Cirsium arvense		1				1
Cirsium vulgare		1				1
Festuca ovina		1				1
Festuca rubra		1				1
Holcus lanatus	1					1
Hypericum perforatum	1					1
Unidentified	1					1
Total no. of seedlings	42	40	46	45	39	212
Total no. of species	14	18	10	9	10	25

SEEDLINGS **HAWTHORN SCRUB**

Species	Trays 1	2	3	4	5	Total
Moehringia trinervia	19	12	15	13	10	69
Poa annua	2	3	1	3		9
Silene dioica	1	3	2		2	8
Stellaria media	1		3	2	1	7
Rubus fruticosus	1	2			2	5
Brachypodium sylvaticum		2		1		3
Carex flacca			1	1	1	3
Fragaria vesca	1		2			3
Stachys sylvatica			3			3
Viola oclorata	1	1		1		3
Campanula rotundifolia				1	1	2
Geranium robertianum			1		1	2
Geum urbanum				2		2
Prunella vulgaris		1		1		2
Sonchus arvensis				1	1	2
Veronica chamaedrys					2	2
Sambucus nigra	1				1	2
Chamaenerion angustifolium		1				1
Cirsium arvense	1					1
Epilobium parviflorum	1					1
Succisa pratensis	1					1
Unidentified		1				1
Total no. of seedlings	30	27	28	26	22	132
Total no. of species	11	8	8	10	10	21

SEEDLINGS

ASH WITH HAWTHORN

Species	Trays 1	2	3	4	5	Total
Moehringia trinervia	22	22	23	21	25	113
Poa trivialis	8	19	21	19	11	78
Urtica dioica	16	18	11	9		54
Silene dioica			3	3		6
Rubus fruticosus		1		1	1	3
Cirsium arvense	2					2
Fragaria vesca			1	1		2
Geranium robertianum			1	1		2
Stellaria media			1	1		2
Chenopodium album	1					1
Cirsium vulgare				1		1
Epilobia sp.					1	1
Ranunculus repens			1			1
Sonchus asper	1					1
Unidentified		2				2
Total no. of seedlings	50	63	62	56	38	269
Total no. of species	6	4	8	9	4	14

SEEDLINGS

ASH WITH SYCAMORE

Species	Trays 1	2	3	4	5	Total
Poa trivialis	106	92	82	91	109	480
Urtica dioica	5	8	5	3	9	30
Betula sp.	7	2	2		5	16
Rubus fruticosus		2	1	2	2	7
Stellaria media	1		2	1	2	6
Stachys sylvatica	1		1			2
Cirsium vulgare			1			1
Geranium robertianum			1	1		2
Geum urbanum		1	1			2
Juncus sp.					1	1
Ranunculus repens	1					1
Rumex crispus					1	1
Senecio vulgaris				1		1
Silene dioica	1					1
Sonchus sp.	1					1
Unidentified				1		1
Total no. of seedlings	123	105	96	100	129	553
Total no. of species	8	5	8	6	7	15

SEEDLINGS

OAK WOODLAND

Species	Trays 1	2	3	4	5	Total
Polygonum aviculare		3	1	4	3	11
Agrostis tenuis			3			3
Chenopodium album		2			1	3
Cirsium vulgare					1	1
Rubus fruticosus		1				1
Silene dioica		1				1
Total no. of seedlings	0	7	4	4	5	20
Total no. of species	0	4	2	1	3	6

Appendix 3 : DETAILS OF VEGETATION COVER AT EACH SAMPLING SITE

QUARRY	Field Cover %
Lotus corniculatus	96
Agrostis stolonifera	48
Plantago lanceolata	37
Festuca ovina	36
Briza media	32
Carex flacca	32
Linum catharticum	16
Dactylis glomerata	14
Rhinanthus minor	12
Dactylorhiza fuchsii	8
Trifolium medium	7
Centaurea scabiosa	6
Holcus lanatus	6
Trifolium pratense	5
Festuca rubra	4
Leontodon hispidus	4
Achillea millefolium	3
Trifolium repens	3
Betonica officinalis	2
Carex nigra	2
Centaurea nigra	2
Hieracium pilosella	2
Plantago media	2
Taraxacum officinale	2
Tussilago farfara	2
Chamaenerion angustifolium	1
Chrysanthemum leucanthemum	1
Fragaria vesca	1
Medicago lupulina	1
Poterium sanguisorba	1
Prunella vulgaris	1

Bellis perennis	t
Blackstonia perfoliata	t
Cerastium arvense	t
Crataegus monogyna	t
Euphrasia ssp.	t
Equisetum arvense	t
Gentianella amarella	t
Hypochoeris radicata	t
Orchis mascula	t
Potentilla sterilis	t
Primula veris	t
Rubus fruticosus	t
Senecio jacobaea	t
Senecio vulgaris	t
Viola hirta	t
Viola riviniana	t
Viola odorata	t

t : plant observed at the site, but not recorded in the quadrats

ARABLE FIELD	Field Cover
	%
Hordeum vulgare	97
Chenopodium album	90
Stellaria media	3
Equisetum arvense	1
Sinapis arvensis	t
Sonchus arvensis	t

GRAZED GRASSLAND	Field Cover %
Trifolium pratense	60
Trifolium repens	56
Plantago lanceolata	54
Holcus lanatus	48
Lolium perenne	48
Agrostis stolonifera	36
Dactylis glomerata	30
Cerastium fontanum	24
Poa trivialis	21
Agrostis tenuis	16
Cirsium arvense	10
Ranunculus repens	10
Lolium	9
Prunella vulgaris	9
Festuca pratensis	8
Phleum pratensis	7
Potentilla reptans	7
Bellis perennis	5
Medicago lupulina	4
Plantago media	4
Rumex crispus	4
Pimpinella saxifraga	3
Centaurea scabiosa	2
Cirsium vulgare	2
Potentilla anserina	2
Senecio jacobaea	2
Trifolium medium	2
Senecio vulgaris	1
Vicia tetrasperma	1
Centaurea nigra	t
Chrysanthemum leucanthemum	t
Galium cruciata	t
Polygonum aviculare	t
Primula veris	t
Ranunculus acris	t
Rumex acetosa	t
Rumex sanguineus	t
Succisa pratensis	t

UNGRAZED GRASSLAND	Field Cover %
Poterium sanguisorba	68
Centaurea scabiosa	40
Carex flacca	40
Plantago lanceolata	34
Centaurea nigra	32
Sieglingia decumbens	30
Leontodon hispidus	29
Lotus corniculatus	28
Festuca rubra	26
Briza media	24
Bromus erectus	24
Dactylis glomerata	20
Succisa pratensis	18
Achillea millefolium	14
Brachypodium sylvaticum	14
Sesleria caerulea	10
Trifolium medium	10
Betonica officinalis	8
Viola riviniana	8
Helictotrichon pratense	6
Holcus lanatus	6
Polygala vulgaris	6
Rubus fruticosus	6
Anthyllis vulneraria	4
Arrhenatherum elatius	4
Crataegus monogyna	4
Hieracium pilosella	4
Linum catharticum	4
Ononis repens	4
Pimpinella saxifraga	3
Agrimonia eupatoria	2
Fragaria vesca	2
Galium verum	2
Leontodon taraxacoides	2
Prunella vulgaris	2
Rhinanthus minor	2
Trifolium pratense	2

Agrostis stolonifera	t
Agrostis tenuis	t
Campanula rotundifolia	t
Carex nigra	t
Chrysanthemum leucanthemum	t
Cirsium arvense	t
Dactylorhiza fuchsii	t
Gymnadenia conopsea	t
Hypericum perforatum	t
Listera ovata	t
Ononis spinosa	t
Orchis mascula	t
Origanum vulgare	t
Primula veris	t
Senecio jacobae	t
Senecio vulgare	t
Sonchus asper	t

GORSE SCRUB	Field Cover
	%
Centaurea scabiosa	27
Centaurea nigra	24
Ulex europaeus	24
Fragaria vesca	20
Rubus fruticosus	20
Brachypodium sylvaticum	14
Carex flacca	14
Festuca rubra	14
Crataegus monogyna	12
Carex nigra	11
Leontodon hispidus	9
Prunella vulgaris	9
Agrostis tenuis	8
Dactylis glomerata	8
Hieracium maculatum	8
Poterium sanguisorba	8
Thymus serpyllum	8
Betonica officinalis	6
Lotus corniculatus	6
Succisa pratensis	6
Viola riviniana	6
Arrhenatherum elatius	5
Plantago lanceolata	5
Polygala vulgaris	5
Primula veris	5
Rosa ssp.	3
Achillea millefolium	2
Cerastium fontanum	2
Trifolium pratense	2
Empty	2
Bellis perennis	t
Campanula rotundifolia	t
Chrysanthemum leucanthemum	t
Dactylorhiza fuchsii	t
Linum catharticum	t
Lolium perenne	t
Orchis mascula	t
Scabiosa columbaria	t
Sieglingia decumbens	t

HAWTHORN SCRUB	Field Cover
	%
Sanicula europaea	47
Geum urbanum	39
Chaerophyllum temulentum	18
Galium aparine	12
Silene dioica	12
Moehringia trinervia	9
Tamus communis	8
Viola odorata	8
Poa trivialis	6
Crataegus monogyna	5
Brachypodium sylvaticum	4
Galium odoratum	4
Geranium robertianum	3
Primula veris	3
Glechoma hederacea	2
Origanum vulgare	2
Veronica chamaedrys	2
Rosa ssp.	2
Arum maculatum	1
Sonchus arvensis	1
Empty	4
Hedera helix	t
Sambucus niger	t
Urtica dioica	t

ASH WITH HAWTHORN	Field Cover
	%
Poa trivialis	51
Geum urbanum	50
Chaerophyllum temulentum	41
Urtica dioica	25
Galium aparine	24
Glechoma hederacea	7
Fraxinus excelsior	3
Crataegus monogyna	3
Heracleum sphondylium	3
Moehringia trinervia	3
Sanicula europaea	3
Arum maculatum	2
Veronica chamaedrys	2
Geranium robertianum	1
Orchis mascula	1
Viola riviniana	1
Empty	1
Primula veris	t
Ribes uva-crispus	t
Rosa sp.	t
Rubus fruticosus	t
Sambucus niger	t
Silene dioica	t

<u>ASH WITH SYCAMORE</u>	<u>Field Cover</u>
	%
Poa trivialis	70
Dactylis glomerata	37
Anemone nemorosa	12
Geranium robertianum	8
Geum riviale	8
Veronica montana	8
Urtica dioica	8
Veronica chamaedrys	6
Fraxinus excelsior	4
Galium aparine	3
Conopodium majus	2
Deschampsia caespitosa	2
Pimpinella saxifraga	2
Vicia sylvatica	1
Empty	2
Acer pseudoplatanus	t
Arum maculatum	t
Betula ssp.	t
Cirsium vulgare	t
Corylus avellana	t
Crataegus monogyna	t
Filipendula ulmaria	t

OAK WOODLAND	Field Cover
	%
Endymion non-scriptus	56
Arrhenatherum elatius	53
Rubus fruticosus	28
Pteridium aquilinum	25
Silene dioica	5
Quercus petraea	4
Anemone nemorosa	2
Glechoma hederacea	2
Fraxinus excelsior	1
Galium aparine	1
Acer pseudoplatanus	1
Empty	5
Coryllus avelana	t

Plate 1a   Quarry site. Ground almost completely vegetated.

Plate 1   Sites on the N side of Cassop Vale

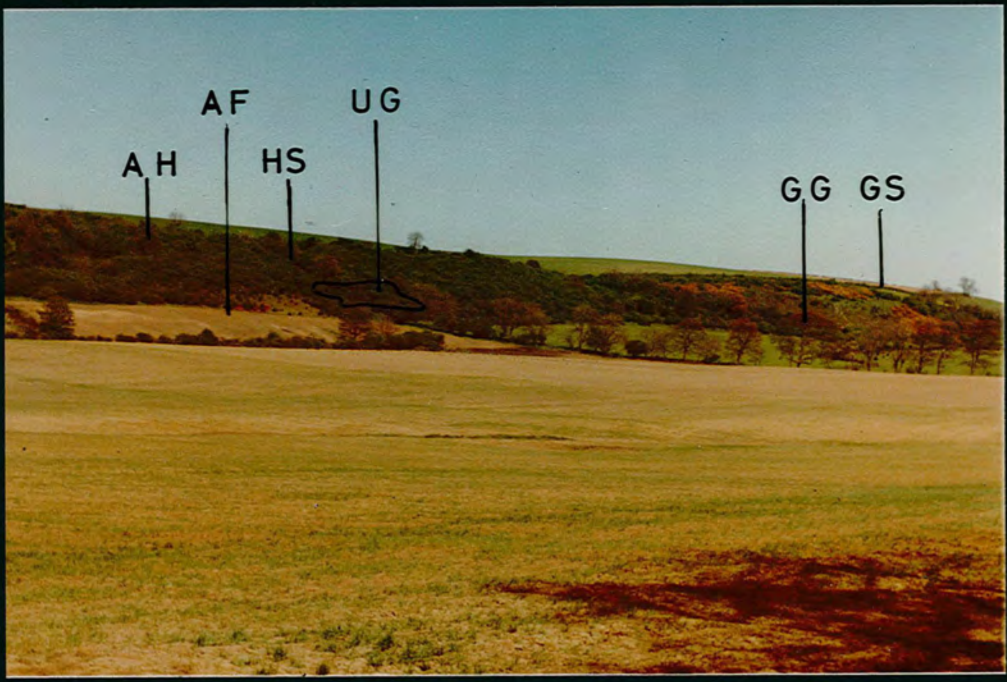

Plate 2 Grazed Grassland and Gorse Scrub
(with the E end of the Hawthorn Scrub)

Plate 3 Ash with Hawthorn (and ploughed field)

Plate 4 Ash / Sycamore on the S side of Cassop Vale

Plate 5 Cattle grazing in the Ash / Sycamore site

Plate 6 Oak Woodland at Castle Eden Dene

Plate 7 Seedling Trays : Arable Field (left) Quarry (right)
The Arable Field is dominated by Chenopodium album.
Compositae spp. and Cirsium spp. occur in the Quarry.

Plate 8 Seedling Trays
Grazed Grassland (left) Ungrazed Grassland (right)

Plate 9 Seedling Trays : Gorse Scrub (left) and Hawthorn Scrub (right)

Plate 10 Seedling Trays : Ash / Hawthorn (left) and Ash / Sycamore (right)

Plate 11 Seedling Trays : Ash/Sycamore (left) and Oak Woodland (right) Seedlings are almost completely absent from the Oak Woodland.